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Factors influencing biodiversity and distributional gradients in mangroves

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Abstract. Numerous factors affect the distribution of mangrove plants. Most mangrove species are typically dispersed by water-buoyant propagules, allowing them to take advantage of estuarine, coastal and ocean currents both to replenish existing stands and to establish new ones. The direction they travel depends on sea currents and land barriers, but the dispersal distance depends on the time that propagules remain buoyant and viable. This is expected to differ for each species. Similarly, each species will also differ in establishment success and growth development rate, and each has tolerance limits and growth responses which are apparently unique. Such attributes are presumably responsible for the characteristic

distributional ranges of each species, as each responds to the environmental, physical and biotic settings they might occupy. In practice, species are often ordered by the interplay of different factors along environmental gradients, and these may conveniently be considered at four geographic scales—global, regional, estuarine and intertidal. We believe these influencing factors act similarly around the world, and to demonstrate this point, we present examples of distributional gradients from the two global biogeographic regions, the Atlantic East Pacific and the Indo-West Pacific.

Key words. Mangrove flora, distribution, environmental controls, dispersal, global biogeography, zonation.

INTRODUCTION

Mangrove habitats have relatively low levels of species richness compared with other high biomass tropical habitats like rain forests and coral reefs (Ricklefs & Latham, 1993). Despite the relatively low biodiversity, plants in these forests have a broad range of structural and functional attributes which promote their survival and propagation in relatively harsh conditions of the intertidal zone. In this sense, diversity of mangrove plants is not measured in terms of numbers of species, but also in terms of the ability of each species to cope with the wide range of environmental conditions in utilizing their individual, specialized attributes. Such

differences are observed in the field where species are presumably ordered along environmental gradients by factors which can be ranked by their degree of importance in different geographic settings.

The importance of such influencing factors is observed where mangrove species group in distinct forest community associations (e.g. Bridgewater, 1989), and where species often have distinct distributional ranges at different geographic scales (e.g. Duke, 1992). For example, mangrove distributions across the intertidal profile are often characterized by distinct zones which border coastlines and channel margins (e.g. Watson, 1928; Macnae, 1968; Lugo & Snedaker, 1974). These zones are apparently comparable throughout the world, altered only by species availability. However, this view needs to be re-assessed in light of recent studies of many intertidal transects in northern Australia. Bunt (1996) found that intertidal species distributions were variable and essentially

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unpredictable. In other studies (e.g. Smith, 1992), animals apparently also influence the distribution and diversity of mangroves. Our concept of relationships between plants and animals has commonly been based on the view that diversity of mangrove plants equates to diversity of structure in mangrove habitats, such that diversity of mangrove plants as habitat and food sources were the links to a dependent fauna. However, as Smith observed, animals appear to complicate distributional patterns of mangrove plants.

The distribution and diversity of mangroves therefore warrants careful re-consideration in view of the apparently wider interplay of influencing factors. In this article, we aim to provide a conceptual model for on-going and future assessments of mangrove distributions by considering distributional gradients at four convenient geographic scales: global, regional, estuarine and intertidal. To do this, we draw on our extensive practical and first-hand knowledge of mangrove habitats from around the world, re-assessing published findings and presenting new information and examples of mangrove distributions from the two global biogeographic regions, the Atlantic East Pacific and the Indo-West Pacific.

FLORISTICS OF MANGROVES

Mangrove vegetation includes a range of functional forms, including trees, shrubs, a palm and a ground fern, generally exceeding 0.5 m in height; and normally growing above mean sea level in the intertidal zone of marine coastal environments, or estuarine margins. Mangrove plants share a number of highly specialized adaptations allowing them to cope with regular tidal inundation of roots and sediments by salty waters. Some well-known characteristics include: exposed breathing roots to grow in anaerobic sediments, support structures of buttresses and above-ground roots to grow with shallow root systems, low water potentials and high intracellular salt concentrations to maintain favourable water relations in saline environments, foliage salt-excretion to remove excess salt from sap, xerophytic water conserving leaves to cope with periods of high salinity stress, and buoyant, viviparous propagules to promote dispersal and establishment of new and existing stands. These specialized attributes are found amongst different species to differing degrees and they are not necessarily found in any single species.

Mangroves comprise a diverse group of plants from

twenty families, from two plant divisions, including the fern family in the Polypodiophyta, and the remainder in the Magnoliophyta, also known as angiosperms. Based on Cronquist (1981), mangrove angiosperms belong to nineteen families from two classes, six subclasses and fourteen orders. Two families are exclusively mangrove, and there are no orders or higher ranks with all mangrove taxa (Duke, 1992). For the Rhizophoraceae, often referred to as the 'true mangrove' family, only four of its sixteen genera inhabit mangroves. Generally, these families are more commonly known in tropical rain forests, and most are pantropic trees and shrubs. Terrestrial relatives are often well-known as garden, timber, fruit or medicinal species. Therefore, although mangroves are highly specialised and adapted to intertidal environments, they are not a genetic entity but an ecological one. The plants are derived from different ancestral sources.

There are twenty-eight genera in total (Table 1), seventeen are exclusively mangrove. There are thirteen polyspecific mangrove genera comprising up to eight species in some, not counting putative hybrids. This relatively low genetic diversity may reflect difficult conditions found in intertidal environments where apparently there is less opportunity for diversification and selection of genetic material. The total number of mangrove species, including putative hybrids, is seventy. Problems with the systematics of mangroves were discussed by Duke (1992). Since then, an additional hybrid *Sonneratia x urama* N.C. Duke was described (Duke, 1994). Major problems persist, however, most notably with the dominant world-wide mangrove genus, *Rhizophora* L.

Mangroves have a range of structures in stature, life form and above-ground roots (Table 1). Each aspect influences both the success and survival of particular species, as well as providing habitat for a wide range of resident and transient fauna. The importance of plant and plant-animal associations cannot be over emphasized in mangrove environments. For example, throughout the world, the network and tangle of prop roots of *Rhizophora* forests often surrounds and provides a seaward/streamside protective mantle for most other mangrove species and associated fauna. In general, floristic diversity equates directly to structural diversity and function. The same factors which limit species presence and growth, will also limit the functions and benefits of particular mangrove stands, such as shoreline stabilization, primary productivity, and habitat for a range of dependent organisms.

Table 1. World occurrence of mangrove taxa in six global biogeographic regions (Fig. 1), common estuarine and intertidal distributions (from Duke, 1992), with brief descriptions of structure and propagules (based on Tomlinson, 1986)

Mangrove flora		Structural character			Global biogeographic regions						Estuary location			Intertidal position			Propagule characteristics			
																	Size (cm ³): 1 = <1; 2 = <1; 3 = <10; 4 = <100; 5 = <1000; 6 = >1000			
Genus	Species	Form	Can	AGR	A	E	P	I	W	P	D	I	U	L	M	H	Form	Shape	Size	Dispersal part
<i>Acanthus</i>	<i>ebracteatus</i>	S	U	—						5 6		I			M	H	Seeds (4) in thin hard capsule	Ovoid	2 (3)	Seeds
	<i>ilicifolius</i>	S	U	—						5 6		I	U		M	H	Seeds (4) in thin hard capsule	Ovoid	2 (3)	Seeds
<i>Acrostichum</i>	<i>aureum</i>	F	U	—	1	2	3	4	5	6		I				H	Paraphyses with numerous spores	Irregular	1	Paraphyses
	<i>danaeifolium</i>	F	U	—	1	2						I	U			H	Paraphyses with numerous spores	Irregular	1	Paraphyses
	<i>speciosum</i>	F	U-C	—						5 6		I				H	Paraphyses with numerous spores	Irregular	1	Paraphyses
<i>Aegialitis</i>	<i>annulata</i>	S	U-C	—						5 6		D			M	H	Crypto-viviparous in thin capsule	Elongate	3	Hypocotyl
	<i>rotundifolia</i>	S	U-C	—						5		?			?		Crypto-viviparous in thin capsule	Elongate	3	Hypocotyl
<i>Aegiceras</i>	<i>corniculatum</i>	S	C	—						5 6		I	U	L			Crypto-viviparous in thin capsule	Elongate	3	Hypocotyl
	<i>floridum</i>	S	C	—						5		?		?			Crypto-viviparous in thin capsule	Elongate	3	Hypocotyl
<i>Aglaia</i>	<i>cucullata</i>	T	C	P						5			U		M					Seeds
<i>Avicennia</i>	<i>alba</i>	T	C	P						5 6		D		L	M		Cotyledon in thin soft pericarp	Conicle	3	Cotyledon
	<i>bicolor</i>	T	C	P	1							D				H	Cotyledon in thin soft pericarp	Ovoid	4	Cotyledon
	<i>germinans</i>	T	C	P	1	2	3					D	I		M	H	Cotyledon in thin soft pericarp	Ovoid	4	Cotyledon
	<i>integra</i>	T	C	P-r						6		I		L			Cotyledon in thin soft pericarp	Ovoid	4	Cotyledon
	<i>marina</i>	S/T	C	P	+1			4	5	6		D	I	L	M	H	Cotyledon in thin soft pericarp	Ovoid	4	Cotyledon
	<i>officinalis</i>	T	C	P						5 6		I		L			Cotyledon in thin soft pericarp	Ovoid	4	Cotyledon
	<i>rumphiana</i>	T	C	P						5 6		D				H	Cotyledon in thin soft pericarp	Ovoid	3	Cotyledon
	<i>schaueriana</i>	T	C	P		2						D			M	H	Cotyledon in thin soft pericarp	Ovoid	4	Cotyledon

Table 1. continued

Mangrove flora		Structural character			Global biogeographic regions						Estuary location			Intertidal position			Propagule characteristics			
																	Size (cm ³): 1 =<1; 2 =<1; 3 =<10; 4 =<100; 5 =<1000; 6 =>1000			
Genus	Species	Form	Can	AGR	A	E	P	I	W	P	D	I	U	L	M	H	Form	Shape	Size	Dispersal part
<i>Bruguiera</i>	<i>cylindrica</i>	T	C	B-k				5	6		D	I			M		Viviparous hypocotyl	Elongate	3	Hypocotyl
	<i>exaristata</i>	S/T	C	B-K						6		I	U			H	Viviparous hypocotyl	Elongate	4	Hypocotyl
	<i>gymnorrhiza</i>	T	C	B-K				4	5	6	D	I			M	H	Viviparous hypocotyl	Elongate	4	Hypocotyl
	<i>hainesii</i>	T	C	B-K					5	6		I				H	Viviparous hypocotyl	Elongate	3	Hypocotyl
	<i>parviflora</i>	T	C	B-K					5	6	D	I			M		Viviparous hypocotyl	Elongate	3	Hypocotyl
	<i>sexangula</i>	T	C	B-K					5	6		I	U		M	H	Viviparous hypocotyl	Elongate	4	Hypocotyl
<i>Camptostemon</i>	<i>philippensis</i>	T	C	–				5				?				H	Crypto-viviparous (2) thin capsule	Ellipsoid	2 (2)	Hypocotyl
	<i>schultzei</i>	T	C	–					6		D	I		L	M		Crypto-viviparous (2) thin capsule	Ellipsoid	2 (2)	Hypocotyl
<i>Ceriops</i>	<i>australis</i>	S/T	C	B						6	D	I				H	Viviparous hypocotyl	Elongate	3	Hypocotyl
	<i>decandra</i>	S/T	U-C	B					5	6		I			M	H	Viviparous hypocotyl	Elongate	4	Hypocotyl
	<i>tagal</i>	S/T	C	B				4	5	6	D	I			M	H	Viviparous hypocotyl	Elongate	4	Hypocotyl
<i>Conocarpus</i>	<i>erectus</i>	S/T	C	–	1	2	3				D					H	Seeds many in hard nut capsule	Ovoid	2 (3)	Capsule
<i>Cynometra</i>	<i>iripa</i>	S	U	–					5	6		I	U			H	Seed in hard capsule	Elliptic	3	Capsule
<i>Diospyros</i>	<i>littoralis</i>	T	C	–						6		I	U		M	H	Seed in berry	Ovoid	3	Seed
<i>Dolichandrone</i>	<i>spathacea</i>	T	C	–					5	6			U		M		Seeds numerous in hard capsule	Linear	3 (5)	Seeds
<i>Excoecaria</i>	<i>agallocha</i>	T	C	K				4?	5	6	D	I	U		M	H	Seeds (3) in hard capsule	3-globule	2 (3)	Seeds
	<i>indica</i>	T	C	K					5		D	I		L	M		Seeds (3) in hard capsule	3-globule	2 (3)	Seeds
<i>Heritiera</i>	<i>fomes</i>	T	C	B					5				U			H	Seed in hard capsule	Ellipsoid	4	Capsule closed
	<i>globosa</i>	T	C	B					5				U			H	Seed in hard capsule	Ellipsoid	4	Capsule closed
	<i>littoralis</i>	T	C	B				4	5	6		I				H	Seed in hard capsule	Ellipsoid	5	Capsule closed
<i>Kandelia</i>	<i>candel</i>	S/T	C	B					5		D			K			Viviparous hypocotyl	Elongate	4	Hypocotyl
<i>Laguncularia</i>	<i>racemosa</i>	S/T	C	k	1	2	3				D	I			M	H	Crypto-viviparous woody capsule	Drupelike	3	Hypocotyl
<i>Lumnitzera</i>	<i>littorea</i>	S/T	C	k					5	6		I			m		Crypto-viviparous woody capsule	Drupelike	3	Hypocotyl
	<i>racemosa</i>	S/T	C	k	4	5	6				D				M	H	Crypto-viviparous woody capsule	Drupelike	3	Hypocotyl
	<i>x rosea</i>	S	C	k					5?	6		I				H	Crypto-viviparous woody capsule	Drupelike	3	Hypocotyl
<i>Mora</i>	<i>oleifera</i>	T	C	B	1								U			H	Cotyledon in thick capsule	Disklike	6	Capsule closed

Table I. continued

Mangrove flora		Structural character			Global biogeographic regions						Estuary location			Intertidal position			Propagule characteristics			
																	Size (cm ³): 1 = <1; 2 = <1; 3 = <10; 4 = <100; 5 = <1000; 6 = >1000			
Genus	Species	Form	Can	AGR	A	E	P	I	W	P	D	I	U	L	M	H	Form	Shape	Size	Dispersal part
<i>Nypa</i>	<i>fruticans</i>	P	C	—		+2	+3		5	6			U	L	M	H	Seed in woody husk	Drupelike	5	Husk intact
<i>Osbornia</i>	<i>octodonta</i>	S/T	C	—					5	6	D				M	H	Seed in calyx	Globose	2	Seed
<i>Pelliciera</i>	<i>rhizophorae</i>	T	U-C	B	1	2						I	U		M	H	Cotyledon in thick corky pericarp	Drupelike	5	Pericarp intact
<i>Pemphis</i>	<i>acidula</i>	S	C	—				4	5	6	D					H	Seeds numerous in hard capsule	Spherical	1 (3)	Seeds
<i>Rhizophora</i>	<i>apiculata</i>	T	C	R					5	6		I				M	Viviparous hypocotyl	Elongate	5	Hypocotyl
	<i>mangle</i>	S/T	C	R	1	2	3				D			L	M		Viviparous hypocotyl	Elongate	5	Hypocotyl
	<i>mucronata</i>	T	C	R				4	5	6		I	U	L	M		Viviparous hypocotyl	Elongate	5	Hypocotyl
	<i>racemosa</i>	T	C	R	1	2	3					I			M		Viviparous hypocotyl	Elongate	5	Hypocotyl
	<i>samoensis</i>	T	C	R					6		D			L	M		Viviparous hypocotyl	Elongate	5	Hypocotyl
	<i>stylosa</i>	S/T	C	R					5	6	D			L	M		Viviparous hypocotyl	Elongate	5	Hypocotyl
	<i>x harrisonii</i>	T	C	R	1	2	3				D	?		L	?		Viviparous hypocotyl	Elongate	5	Hypocotyl
	<i>x lamarckii</i>	T	C	R					5	6	D	I			M		Viviparous hypocotyl	Elongate	5	Hypocotyl
	<i>x selala</i>	T	C	R					6		?				?		Viviparous hypocotyl	Elongate	5	Hypocotyl
<i>Scyphiphora</i>	<i>hydrophyllacea</i>	S	U-C	—					5	6		I				H	Seeds (4) in woody calyx	Drupelike	1 (2)	Calyx intact
<i>Sonneratia</i>	<i>alba</i>	T	C	P				4	5	6	D			L			Seeds numerous in leathery berry	Globose	2 (4)	Seeds
	<i>apetala</i>	T	C	P					5				U	L	M		Seeds numerous in leathery berry	Globose	2 (4)	Seeds
	<i>caseolaris</i>	T	C	P					5	6			U	L			Seeds numerous in leathery berry	Globose	2 (5)	Seeds
	<i>griffithii</i>	T	C	P					5		D			L			Seeds numerous in leathery berry	Globose	2 (4)	Seeds
	<i>lanceolata</i>	T	C	P					5	6			U	L			Seeds numerous in leathery berry	Globose	2 (5)	Seeds
	<i>ovata</i>	T	C	P					5	6	D				H		Seeds numerous in leathery berry	Globose	2 (5)	Seeds
	<i>x guilgai</i>	T	C	P					5	6		I		L	M		Seeds numerous in leathery berry	Globose	2 (4)	Seeds
	<i>x urama</i>	T	C	P					5?	6		I			M		Seeds numerous in leathery berry	Globose	2 (4)	Seeds
	<i>alba x ovata</i>	T	C	P					5		?				?		Seeds numerous in leathery berry	Globose		Seeds
<i>Tabebuia</i>	<i>palustris</i>	S	U	—	1								U	L	M		Seeds numerous in hard capsule	Linear	3	Seeds
<i>Xylocarpus</i>	<i>granatum</i>	T	C	B				4	5	6		I			M	H	Seeds (8-10) in woody capsule	Globose	5 (6)	Seeds-tetrahedral
	<i>mekongensis</i>	T	C	K-P					5	6		I			M	H	Seeds (6-7) in woody capsule	Globose	4 (5)	Seeds-tetrahedral
Total spp.	By region =				13	11	8	11	51	47										

Life form (Form): T = tree; S = shrub; P = palm; F = ground fen. Global regions: 1 = W. America; 2 = E. America; 3 = W. Africa; 4 = E. Africa; 5 = Indo-Malesia; 6 = Australasia; + = introduced. Canopy position (Can): C = canopy; U = under canopy. Above-ground roots (AGR): R = prop roots; P = pneumatophores; B = buttresses; K = knee roots. (lower case = diminutive form). Upriver location: D = downstream; I = intermediate; U = upstream. Tidal (above Mean Sea Level) position: L = low intertidal; M = medium intertidal; H = high intertidal.

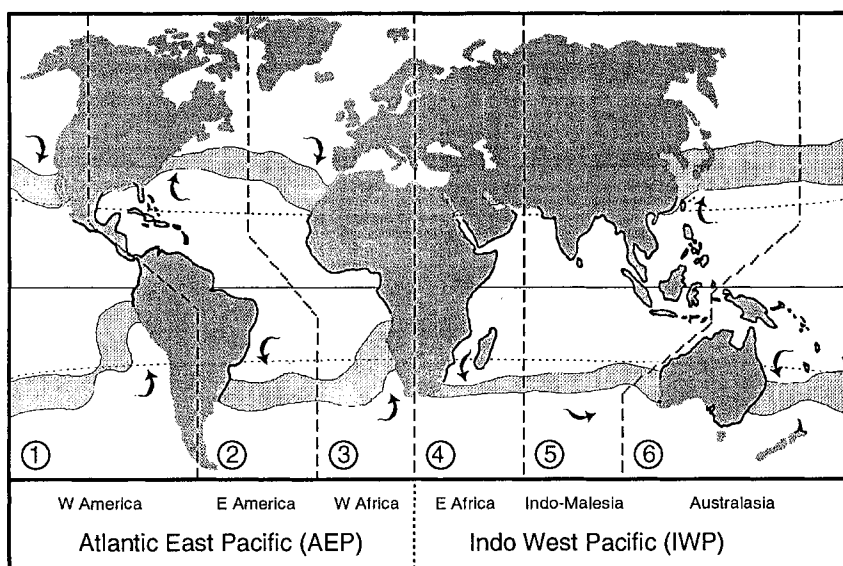


Fig. 1. World distribution of mangroves (solid coastlines) showing extent within six biogeographic regions (Duke, 1992). The poleward extent of mangroves is usually associated with the winter position of the 20°C isotherm (range of summer and winter positions shown) and this is influenced by ocean currents (shown by arrows).

FACTORS INFLUENCING SPECIES RICHNESS OF MANGROVES

The distribution of mangroves may be assessed according to four geographic scales, namely their occurrence throughout the world in one or more biogeographic regions, their coastal range within each region, their upstream location within an estuary, and their position along the intertidal profile. We review the chief factors which influence species richness and distribution at these four scales. Many factors apply at more than one scale, but in each case it is useful to draw out the subtle distinctions.

Global distributional gradients—inter-regional differences

Mangrove plants are found throughout the world in tropical regions and occasionally in subtropical latitudes. No species occur only in subtropical environments. In Table 1, the broad distributional ranges of each species are listed, based on their presence or absence in six biogeographic regions (Fig. 1): (1) western Americas and the eastern Pacific, (2) eastern

Americas and the Caribbean, (3) western Africa, (4) eastern Africa and Madagascar, (5) Indo-Malesia and Asia, and (6) Australasia and the western Pacific. Mangrove species are divided primarily, however, into two global hemispheres, the Atlantic East Pacific (AEP), and the Indo-West Pacific (IWP). The species diversity is greater in the IWP, with a total of fifty-eight taxa, more than four times more than the AEP, with thirteen naturally occurring species. There is an overlap of only one species between hemispheres, namely *Acrostichum aureum* L., a mangrove fern. It is also possible that *Rhizophora samoensis* (Hochr.) Salvo is the same species as *R. mangle* L. (Ellison, 1991) but this remains to be shown (Tomlinson, 1986; Duke, 1992). The diversity of genera in these families is relatively conservative, with eight genera in the AEP and twenty-three in the IWP. There are three genera in common and these occur throughout the six regions. Apart from the Pellicieraceae, families in the AEP are a subset of those in the IWP. The region with fewest species is western Africa (region 3), in the AEP. It has seven species, whilst Indo-Malesia (region 5) in the IWP, has more than forty-nine. In the IWP, the east African region is the most depauperate with only ten species.

Global importance of temperature

Temperature limits species to essentially tropical latitudes, although one species, *Avicennia marina* (Forsk.) Vierh., extends far into the temperate zone of southern Australia. Global distributions of mangroves are limited chiefly by the physiological tolerance of each species to low temperature, marked by their different poleward limits. For example, viable *Rhizophora mangle* propagules from Mexico routinely reach beaches and estuaries of southern Texas. Some become established only to be killed during severe winter freezes (Sherrod, Hockday & McMillan, 1986).

Mangroves are restricted generally to areas where mean air temperatures of the coldest months are higher than 20°C, and where the seasonal range does not exceed 10°C (Walsh, 1974; Chapman, 1975, 1977): the limits to their poleward extents are often marked by the incidence of ground frost. As a general pattern, the winter position of the 20°C isotherm for sea water closely matches the poleward extent of mangroves in each hemisphere (Fig. 1). Deviations from otherwise tropical distributions mostly correlate with warm and cold oceanic currents, such that distributional ranges tend to be broader on eastern continental margins than on western coastlines.

There are at least three notable discrepancies from the above pattern with water temperature, and these all occur in the southern hemisphere; notably along the coastlines of eastern South America, around Australia, and across the North Island of New Zealand. This could be the result of specific, small-scale extensions of irregular warm currents affecting present day distributions, but it is more likely to be evidence of relict populations, representing refuges of greater poleward distributions in the past. Some populations at higher latitudes are also genetically distinct from populations in tropical parts of the range, notably *Avicennia marina* var. *australasica* (Walp.) Moldenke ex N.C. Duke in south-eastern Australia (Duke, 1995).

Global importance of suitable habitat and climate

The influence of precipitation and temperature on mangrove distributions were analysed by Blasco (1984). He reported four classification groupings: (1) warm humid areas where 90% of the world's mangroves are found, notably from South Mexico to Colombia, in the Caribbean, North Brazil, and from S.E. Asia to N. Queensland (Australia); (2) sub-humid areas where mangroves are occasionally found, such as East Africa,

India, S. Queensland (Australia), Mexico and Venezuela; (3) semi-arid areas where mangroves are rarely found, usually close to major river mouths, such as the Indus Delta (Pakistan), Gujarat (India), the Western and Northern Territory provinces of Australia, and Ecuador; and, (4) arid areas where mangroves are practically unknown, except where there are winter rains, for example along the Ethiopian and Egyptian coastlines of the Red Sea, the Persian Gulf and the Gulf of California.

In equatorial and tropical summer rainfall regions, mangroves are tall, dense and floristically diverse. In subtropical arid regions mangroves are low, scattered and sporadic. Areas of higher coastal rainfall and high riverine inputs of freshwater tend to support more diverse communities of mangroves than areas of low coastal rainfall and limited runoff. This is shown in Australia, where at 22.5°S (Tropic of Capricorn) there are four species on the dry west coast and twenty species on the wet east coast (Tomlinson, 1986; Duke, 1992; also see Fig. 2). On the eastern coastline, the tallest (up to 35 m tall) and more dense forests of mangroves inhabit areas where mean annual rainfall is >1500 mm and distributed throughout the year. In areas where rainfall is <1500 mm and seasonal, mangroves are much shorter, around 1–6 m. In these drier areas, there are also larger vegetation-free zones bordering the landward fringes (Fosberg, 1961; Macnae, 1966). In general, the suitability of habitat for particular mangrove species depends on climatic conditions and the coastal geography.

Global importance of dispersal and establishment of propagules

Most mangrove species have buoyant, water-borne propagules. The present dispersal of these propagules is constrained by land masses blocking current flow, and by wide bodies of water. Such limitations on dispersal usually confines species to particular regions, depending on their dispersive range and their ability to become established in new locations. In order to establish new colonies and to extend existing distributional ranges, species would need to 'hop' across or around either larger bodies of water or land. The effective range of each species depends on a number of factors including: the number of days propagules remain buoyant and viable, the rate of surface currents, the water conditions, and the availability of suitable habitats. Flotation times, observed in experimental trials, vary from a few days (*Laguncularia* Gaertn.f.

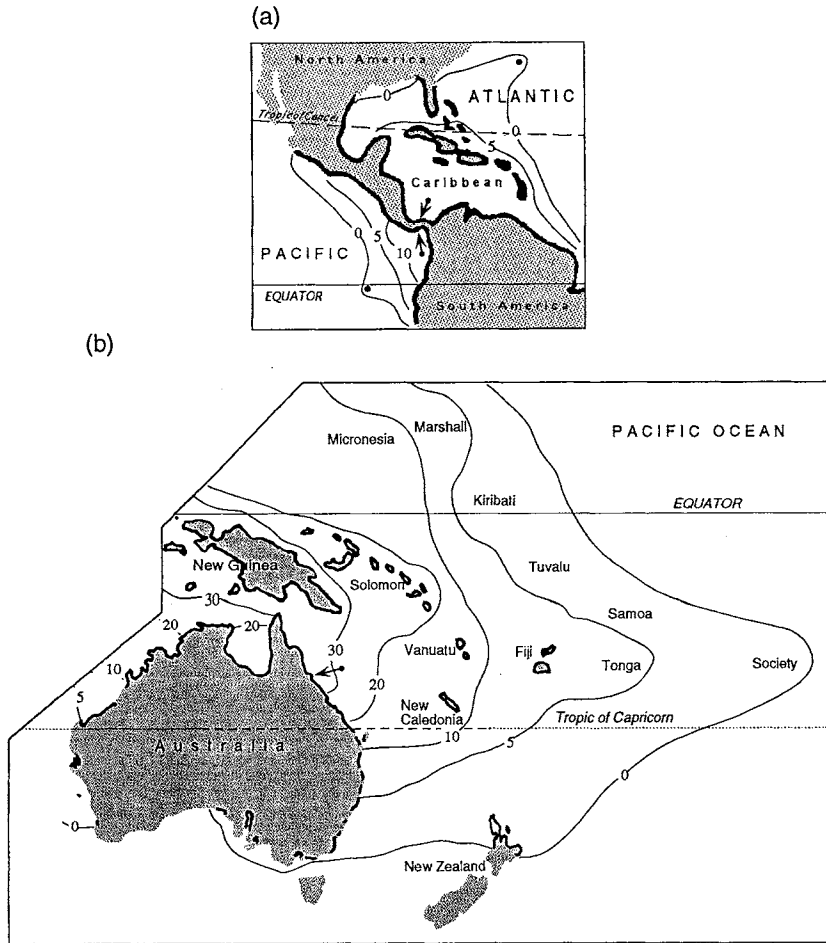


Fig. 2. Regional distributional gradients of mangroves for three biogeographic regions (references in Spalding *et al.* 1997): (a) East and West American regions of the AEP; and (b) the Australasian region from the IWP. Isoclines define the geographic extent of maximal numbers of mangrove species from stands along continental margins to island enclaves. Solid coastlines describe the general occurrence of mangroves in each region. Arrows with dots mark locations of local scale distribution gradients referred to in the text and in Figs 4 and 5. Solid dots in (a) mark the positions of the islands of Bermuda and Galapagos, respectively.

and *Avicennia marina*, to many months (*Rhizophora* sp. and *Avicennia germinans* (L.) Stearn) (e.g. Steinke, 1975, 1986; Rabinowitz, 1978). Flotation time may also increase with decreased water temperature (Steinke & Naidoo, 1991) and decreased water salinity (e.g. Rabinowitz, 1978). Currents also vary considerably in rate and direction, changing in these respects with climate, weather conditions, seasons, and annual changes. Colder temperatures and the lack of suitable habitat also serve to limit propagule viability and establishment success.

Global importance of continental drift and tectonic events

Mangrove distributions are not only influenced by long distance dispersal and establishment success, but also by geographical conditions and past changes in these conditions. Barriers chiefly include land masses (blocking dispersal of water-borne buoyant propagules), wide expanses of water (lack of suitable habitat), and low temperature (physiological limits of species). Currently, there are four major barriers

influencing the dispersal of warm shallow-water marine organisms (Briggs, 1974), including the continental land masses of Africa and Euro-Asia, North and South American continents, North and South Atlantic Oceans, and the eastern Pacific Ocean. Two barriers appear to be effective during recent geological time, namely the African Euro-Asian continents, and the Pacific Ocean. Thus, mangrove species, along with other tropical biota of shallow-water marine habitats, are divided into two global hemispheres. The discontinuous global range of key mangrove genera is indicative of an earlier shared dispersive range. Within the AEP, there are fewer species and genera, although the current distributions of several mangrove species span two extant barriers. By contrast, the diverse IWP flora has few present-day barriers. Current global distributions cannot be explained in the context of present arrangements of land and water masses.

Tectonic movements of emergent lands have apparently greatly influenced the present day distribution of species. Geological and climatic conditions must have changed, rather than genetic make-up and physiological requirements of mangrove plants, since their characteristics are common around the world despite their current genetic isolation. Plant species comprising mangrove ecosystems are derived from a variety of ancestral groups, and their co-occurrence in the present time cannot not be taken as a measure of common evolution or origin (Duke, 1995). Changes taking place in this habitat were apparently greatly influenced by the massive displacement of continents during the last 100 million years. Mangrove evolution, diversification and dispersal apparently were accelerated by continental drift.

The discontinuous range of seven widely-occurring mangrove species in the AEP, from the Pacific coast of America to West Africa, can only be explained in the context of geological change, such as the opening of the Central American isthmus, and a widening of the Atlantic Ocean. Furthermore, the disjunct range of *Rhizophora samoensis* in the South-Western Pacific (IWP), and its close relative, *R. mangle* in the Eastern Pacific (AEP), suggests an ancient connection across the southern Pacific Ocean. The species possibly made the crossing via an ancient island archipelago formed during the development of the Pacific Plate (Schlanger & Premoli-Silva, 1981; Schlanger, Jenkyns & Premoli-Silva, 1981). This putative migration was apparently only one-way, to the west. It also appears that the distances between ancient islands must have been

relatively large since only the highly dispersive species, *Rhizophora mangle*, apparently made the crossing.

Regional distributional gradients— intra-regional differences

Gradients in mangrove species richness are found within all biogeographic regions (e.g. Tomlinson, 1986; Hutchings & Saenger, 1987). Based on recent improvements in distributional records (e.g. Duke, 1992; Spalding, Blasco & Field, 1997) and the personal knowledge of each author, we offer a refined description of biodiversity gradients within two biogeographic regions: (1) the West and East American regions of the AEP; and (2) the Australasian region of the IWP. These examples serve both to demonstrate our observations of species distributions, and to identify common elements between regions based on the most likely factors influencing distributions at this scale.

In the West and East American region (Fig. 2a), there are thirteen naturally-occurring species and two introduced ones (Table 1). Distributional gradients in this region appear relatively simple, and feature a decline in species richness with increasing latitude, and from west to east coasts of the Central American isthmus. Mangrove biodiversity in the AEP is maximal on the Pacific coasts of Colombia, Panama and Costa Rica. One group of species is found throughout the AEP including: *Avicennia germinans*, *Acrostichum* spp. (apparently two species, but records are not sufficient to distinguish them), *Conocarpus erectus* L., *Laguncularia racemosa* (L.) Gaertn.f., *Rhizophora mangle*, *R. racemosa* Meyer and *R. x harrisonii* Leechman. At the West African end of the range, there are no additional native species, but in the American east and west regions, mangroves are characterized by an additional small group of restricted-range species. Three species, *Avicennia bicolor* Standley, *Pelliciera rhizophorae* Triana & Planchon, and *Mora oleifera* (Triana) Ducke, are essentially restricted to the Pacific coast, although *Pelliciera* Planchon & Triana is also found in isolated stands on the Caribbean side of Panama, Colombia, and possibly Nicaragua. On the Atlantic coast, there is only one species, *Avicennia schaueriana* Stapf & Leechman ex Moldenke, which occurs from the Lesser Antilles and Venezuela south along the east Atlantic coast of South America to Brazil. There are no additional species in the western Caribbean.

By contrast, the mangrove flora of the Australasian region (Fig. 2b) is one of the richest in the world, with forty-seven species in twenty-one genera (Table 1). Two

Indo-Malesian genera, *Aglaia* (Roxb.) Pellegrin and *Kandelia* Wight & Arnold, are absent but another, *Diospyros* L. (Duke, Birch & Williams, 1981), is apparently unique to this region. There are seven endemic taxa (including six species and one putative hybrid) in Australasia, compared with eleven in Indo-Malesia. *Rhizophora samoensis* and *R. x selala* (Salvosa) Tomlinson are located only in the east, on several south-western Pacific islands, including New Caledonia, Fiji, Tonga and Samoa (Tomlinson, 1978; Ellison, in press). This is particularly noteworthy since no other species have similarly disjunct distributions, and it is of great interest that *R. samoensis* is closely related to *R. mangle*, which is so widespread in the AEP. The common trend otherwise is for species of the IWP flora to range eastward by varying degrees, with a notable decline in species numbers across the western Pacific, and projecting further east in the southern hemisphere (see Fig 2b). Species numbers also decline with increasing latitude south especially along the east and west coasts of Australia.

The distributional gradient eastward across the South-Western Pacific dominates the region (Fig. 2b). In the west, New Guinea has the greatest diversity of mangroves in the world, owing to its location bordering Indo-Malesian and Australasian centres of diversity (Duke, 1992). There are forty-three species in New Guinea and thirty-nine in northern Australia. Immediately east, in the Solomon Islands there are twenty-two, while in Vanuatu there are fourteen species. Three species extend south of the Solomons to New Caledonia. New Caledonia and Micronesia have fourteen species each. Nauru has only one species, *Bruguiera gymnorrhiza* (L.) Lamk. Kiribati has four species. The Marshall Islands have five species. Tuvalu has two species. Seven species from the eastern Australasian flora extend to their eastern distributional limits in Polynesia. These characterize the low diversity mangroves in Fiji, Tonga and Samoa. Fiji and Tonga have eight species each, and Samoa has three. The most widely-distributed mangrove species in the Pacific is *Bruguiera gymnorrhiza*, occurring in all Pacific island mangrove communities except for the northern Ryukyus (Japan) and the southern limit of New Zealand. *Lumnitzera littorea* (Jack) Voigt. has the second largest range, not occurring in the Samoan group, or the southern Gilbert Islands of Kiribati (Fosberg, 1975). *Rhizophora stylosa* Griff. does not occur in Micronesia with the exception of Guam (Fosberg, 1975), yet extends south of the equator to Tuvalu and Tonga but not to Samoa.

At the eastern limit of mangroves in Polynesia, the low diversity of mangrove species equates to some notable changes in community structure and microhabitat. In the absence of higher intertidal specialists, such as *Ceriops* Arnold., *Excoecaria agallocha* becomes more common in mangrove communities of Polynesia, forming unusual, extensive monospecific stands. In Tonga, *Excoecaria* L. forests dominate the mangrove area. In Samoa, *Bruguiera gymnorrhiza* occupies most of the mangrove area, and the lack of high intertidal plants may also explain the rare occurrence of tropical estuarine marshes (Whistler, 1976). These observations imply that habitat availability is not a limitation on these islands.

Mangroves have been introduced in several Pacific islands to the east and north of the present natural limit. *Rhizophora mangle* was introduced to Enewetak in 1954 (St John, 1960). In Hawaii, *Rhizophora mangle* was introduced in 1902 to Molokai and Oahu, and *Bruguiera sexangula* was introduced in 1922 to Oahu (identification confirmed by NCD). Both are well established today (Wester, 1982). Other species were introduced in 1922 but did not become established, including: *Rhizophora mucronata* last recorded in 1928; *Bruguiera parviflora* last recorded in 1948; and *Ceriops tagal* (Perr.) C.B. Robinson not recorded after 1922. In French Polynesia, there are small areas of *Rhizophora stylosa* on Moorea and Bora Bora. It is not certain whether this species was introduced (Fosberg, 1992) or whether it is native (Taylor, 1979; Ellison, in press).

Regional importance of dispersal capabilities

Dispersal of mangroves between river systems and locations within regions depends directly on the long-range dispersal capability of each species. Table 1 lists the range of mangrove propagules including: fern spores, small and large seeds in soft and hard capsules, several crypto-viviparous forms, and a range of small and large viviparous hypocotyls. This mixed group is expected to have quite different dispersal/establishment capabilities.

Ellison (1996) recently reported on tests of flotation properties of *Rhizophora mangle* propagules, making inferences with respect to mangrove distributions in the East American region. In flowing ocean water experimental systems, it was found that most propagules floated for over three months. Rabinowitz (1978) obtained similar results, with propagules being reported to float for at least 40 days. Davis (1940), however, reported propagules floating after more than

one year. Rabinowitz reported that *Avicennia germinans* floated for at least 14 days and up to 110 days, while *Laguncularia racemosa* was unable to take root if immersed for more than 8 days. Although establishment success was not reported for *Rhizophora* or *Avicennia* L., there was sufficient evidence to speculate that viable propagules of *Rhizophora* and *Avicennia* might reach Bermuda in the north Atlantic from the Caribbean, but that those of *Laguncularia* could not (see Fig. 2a). This was used to explain the present day absence of *Laguncularia* in Bermuda (Ellison, 1996). However, such deductions require cautious interpretation in view of the observations by Banus & Kolehmainen (1975), who found that roots of *R. mangle* propagules developed within 10 to 17 days of falling from the parent tree, and leaves expanded after 40–50 days. This occurred irrespective of availability/proximity of suitable substrates (see also Davis, 1940). The longevity of propagules is also influenced by salinity (Rabinowitz, 1978) and water temperature (Steinke & Naidoo, 1991). For these reasons, additional experiments are required, such as: (1) to score floating duration and condition; as well as, (2) to determine establishment success (viability) at set intervals during flotation trials.

Similarly, the dispersal ranges of species in the South-Western Pacific are probably much more restricted than generally perceived. While there are no obvious barriers to dispersal of propagules within this region, apart from the waters between islands, there are notable distributional discontinuities and ranges for some species. Species appear unable to disperse to, and/or to establish on, many of the eastward South-Western Pacific islands, especially those to the east of Tonga and Samoa. Mangroves are absent on these islands despite there being suitable climate and habitat for mangroves. The discontinuity of *R. samoensis* within this range is also curious. It is possible that IWP species are limited by a combination of factors, but primarily by dispersal range. *Bruguiera gymnorrhiza* appears to be the most successful dispersive species, with its broad distributional range throughout the IWP.

Regional importance of temperature, rainfall, catchment area and tides

Dispersal success must also be considered in terms of habitat availability. At the regional scale, suitability of habitat depends on environmental factors like estuary size, rainfall and tides. Estuary size is understandably limiting on oceanic islands. Species richness also

declines generally with increasing latitude on north-south coastlines of the two regional examples (Fig. 2). Similar declines with latitude are also observed for north-south transects through respective groupings of islands, although in the South-Western Pacific maximum diversity does not centre on the equator.

In Australia, mangroves are distributed around most of the mainland coast, but their richness and extent is greatest in the tropical north. Duke (1992) described two notable patterns, one with latitude and the other with rainfall. Areas of higher rainfall are patchy in Australia, and these areas are characterized by increased numbers of species in affected river systems. For example, in Fig. 2b, the relatively dry coastline of the Gulf of Carpentaria in north Australia has fewer than twenty species despite higher numbers being recorded both in the east and west, and to the north in New Guinea. Two major environmental factors, temperature and rainfall, partly explain regional distributions of mangroves. Low temperatures restrict the latitudinal extent of different species in different ways, and areas of higher rainfall usually have greater numbers of species. Species richness in mangrove forests is often greatest in wet equatorial areas.

Species richness and environmental factors have been examined in several neighbouring estuarine sites around northern Australia. It was found that local species diversity was often higher in estuaries which were longer, with larger catchment areas, as well as in those in areas of higher rainfall (Bunt, Duke & Williams, 1982a; Smith & Duke, 1987; Duke, 1992). The influence of rainfall, therefore, not only comes from rain falling directly on mangroves, but also as a result of runoff from riverine catchments (cf. Ewel *et al.*, 1998). Fig. 3 shows the relationship between species numbers and mean annual rainfall, where species richness is greatest in larger estuaries in areas of moderate-high annual rainfall (~2000 mm). From such findings, it has been shown that species richness is greatest in moderated salinity regimes indicating the importance of interacting factors such as the amount, duration, frequency and regularity of runoff (cf. Ball, 1998).

There appears to be a similar interplay between species richness and environmental factors in the West and East American region. This was shown partly by the occurrence of the west to east decline in numbers of species (Fig. 2a), and partly by the distributions of particular species, notably those with restricted ranges. Although comparable system-by-system environmental data, as reported for Australian estuaries, are lacking,

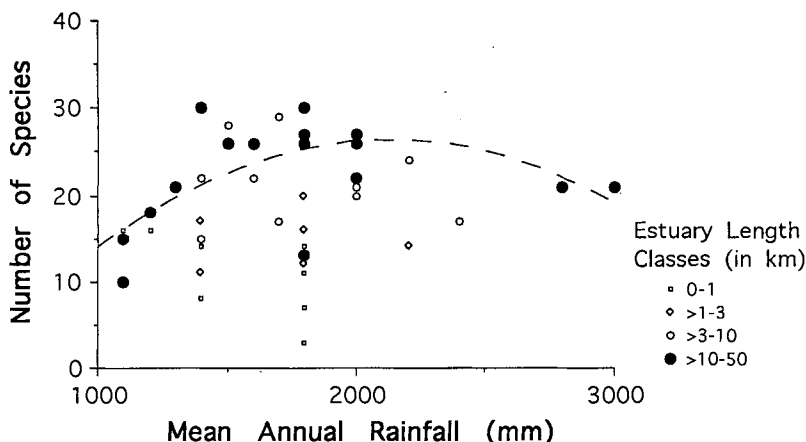


Fig. 3. A plot of numbers of mangrove species and mean annual rainfall shows the relationship between species richness and rainfall in northern Australia. The curve fit shown represents a significant correlation for a second order polynomial ($r^2 = 0.370$, $n = 16$, $P < 0.01^{**}$) based on species checklists for larger estuaries (>10 km in length) (adapted from Duke, 1992).

it is possible to make extrapolations using available distributional records and preliminary field surveys (e.g. Duke, Pinzón & Prada, 1993). The current dispersal barrier between Pacific and Atlantic mangroves, the Central American isthmus, does not appear to be the only factor restricting Pacific species to one side. One species, *Pelliciera*, does occur on both coasts, but it has a rather restricted present day distribution eastward, especially considering that its range was much further eastward in the past (e.g. Jiménez, 1984). *Rhizophora racemosa* is also found in both West and East American regions, and in West Africa, but it does not occur on the immediate Atlantic coast of Central America. It is also unlikely that any of the Pacific species evolved after the current dispersal barrier was formed, approximately 3 million years ago. It is proposed, therefore, that these species, particularly those on the Pacific coast, were lost from the easterly sites of the East American region when environmental conditions became unsuitable for them. This may have occurred before or after the isthmus formed.

If this is true, these species might be expected to have more limited abilities to cope with change, compared to those of the widely-occurring group. Again, evidence is lacking, but there are indications that the restricted-range species have relatively limiting characteristics, including: the upstream estuarine habitat requirements of *Mora*, which appears to restrict it to larger freshwater-dominated estuaries (e.g. see also Figs 4b

& 5a); *Avicennia bicolor*, which tends to occur in larger estuaries; and *Pelliciera*, which has relatively poor dispersal ability (Rabinowitz, 1978) and occurs chiefly in freshwater-dominated estuaries (Duke *et al.*, 1993). Furthermore, the distribution of *Rhizophora racemosa* is patchy, and it also appears limited to larger, freshwater-dominated estuaries, although it is apparently much less limited than restricted-range species. In support of this view, *R. racemosa* appears to be characterised (limited) by an intermediate estuarine distribution in river systems on the Pacific coast from Colombia to Costa Rica (e.g. see also Figs 4b and 5a), and it is absent in smaller systems (Duke *et al.*, 1993). Several of these comments indicate the importance of estuarine position, determining species vulnerability when faced with changing climate and other influences.

In Australian studies (Smith & Duke, 1987; Duke, 1992), tidal variation was also considered, but the effect of tides was not clear since there were insufficient sites from a wide range of tidal regimes. There was also a confounding effect from interactions with other factors, such as rainfall. In the Central American–Caribbean area, the importance of tidal influences on distributions of each species are not known either, but they are likely to be significant given the notable differences observed in the area. In each area, however, a small tidal variation may also contribute to lower species richness. For example, species richness is relatively low in both the eastern Caribbean and the Gulf of Carpentaria,

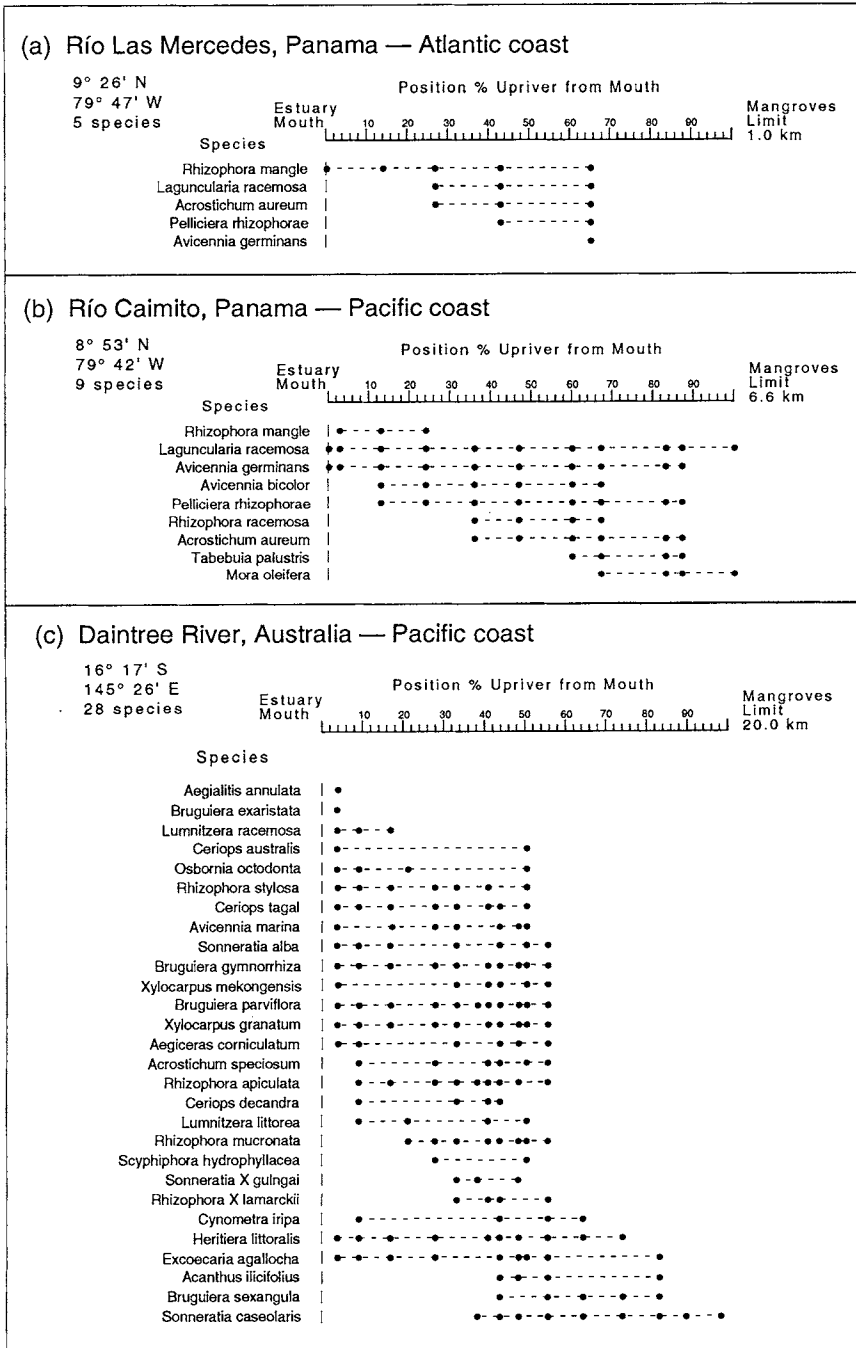
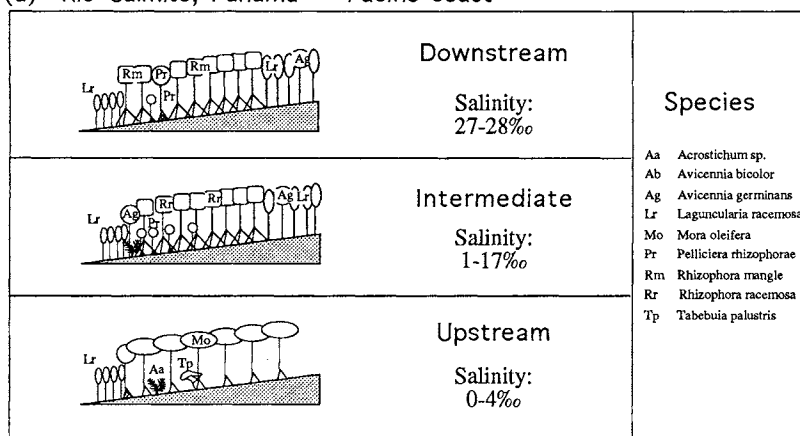


Fig. 4. Upstream estuarine distributional ranges of mangroves in three freshwater-dominated river systems from three biogeographic regions (Duke *et al.*, 1993; Duke, unpubl. data): (a) Río Las Mercedes, East American region, AEP (see Fig. 2a); (b) Río Caimito, West American region, AEP (see Fig. 2a); and (c) Daintree River, Australasian region, IWP (see Fig. 2b). Note: dots mark species presence at sites along the major tributary.

(a) Río Caimito, Panama — Pacific coast



(b) Daintree River, Australia — Pacific coast

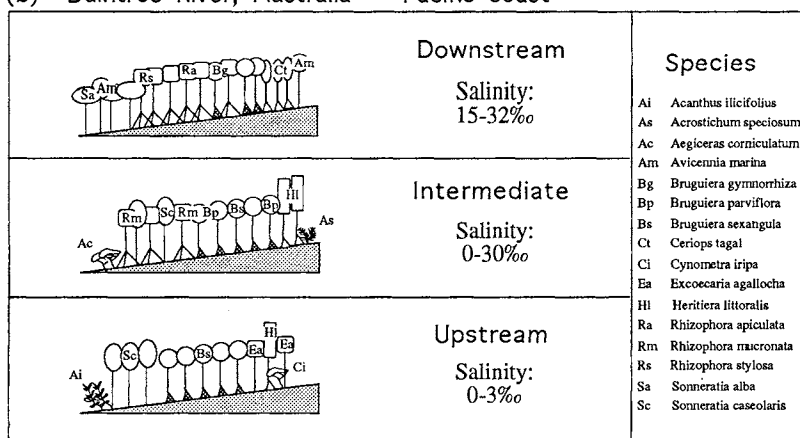


Fig. 5. Intertidal distributional gradients for three upstream estuarine locations in two freshwater-dominated river systems from two biogeographic regions (Duke, unpubl. data): (a) Río Caimito, West American region, AEP (see Fig. 2a); and (b) Daintree River, Australasian region, IWP (see Fig. 2b). Salinities noted are indicative of annual ranges.

Australia (see Fig. 2). In the Gulf of Carpenaria, factors limiting species richness may include a combination of drier climate, discussed earlier, as well as the small tidal variation.

Upstream distributional gradients—distributions within estuaries

The spatial distribution of mangrove species within an estuarine system can be classified into three categories: downstream, intermediate and upstream (Table 1). This applies particularly to freshwater-dominated systems.

A proportional distance from the mouth of the estuary can be used to classify position upriver, where 'downstream' represents the lower third of the estuary (including non-estuarine stands), 'intermediate' represents the middle third of the estuary, and 'upstream' represents the upper third. Downstream and upstream categories are useful in identifying river systems characterized by the presence of particular mangrove species. For example, a species might be known as either an upstream or downstream specialist, or both, and species can be ordered by their occurrence within the estuarine system. In Fig. 4, three examples

of upriver distributions from the biogeographic regions, West and East America, and Australasia, show that these characteristics apply world-wide. Floristic diversity therefore depends not only on available species, but also on factors which influence estuarine systems, namely catchment size, estuary length, rainfall, and tidal variation.

The importance of salinity along estuaries

Studies in Australia show the importance of the various physical and climatic factors in relation to salinity (Bunt, Williams & Clay, 1982b; Ball, 1988; Ball & Pidsley, 1988, 1995; Duke, 1992). The physiological tolerance of each species to salinity influences its estuarine range such that each might be characterized in terms of either, or both, upstream or downstream limits. For example, Duke (1992) showed that in Australia, *Sonneratia alba* is a downstream species reaching upstream to some limit which is different for each estuarine system, e.g. the range of this species in the Daintree River is from 0 to 55% upriver (Fig. 4c). By contrast, *Sonneratia caseolaris* occurs upstream, e.g. the range of this species in the Daintree River is from 40 to 100% upriver (Fig. 4c). Both *S. caseolaris* and *S. lanceolata* are upstream species, and they only occur in freshwater-dominated systems. The estuarine ranges of these species extend downstream from the upstream limit of mangroves to some downstream limit, depending on the river system. An assessment of another genus, *Avicennia*, showed a different distribution of species in the same region. *Avicennia marina* is located at the mouths of most estuaries and reaches the upstream tidal limits in most, excepting east coast systems which are strongly freshwater-dominated, e.g. the range of this species in the Daintree River is from 0 to 50% upriver (Fig. 4c). However, in northern Australian sites of larger estuaries, *A. integra* occurs together with *A. marina*, and the entire upriver distribution of *A. integra* is within the range of *A. marina*.

Similar patterns in estuarine distribution described for Australian rivers were also observed in freshwater-dominated river systems in Central America (e.g. see Fig. 4b). In this area, and particularly on the Pacific coast from Costa Rica to Colombia, *Rhizophora mangle* occurs in the downstream sector, *Avicennia germinans* occurs in downstream and intermediate sectors, *A. bicolor*, *Pelliciera* and *R. racemosa* occur in the intermediate sector, *Mora* occurs in the upstream

sector, and *Laguncularia* occurs throughout the entire estuary.

The factors underlying estuarine upstream distributions in Australia have been assessed in correlative studies of estuarine gradients and environmental factors, including salinity (Duke, 1992). The upstream position of the salinity gradient reflects changes between wet and dry seasons. Salinity levels within Australian estuaries were found to be a function of several factors, notably annual rainfall, tidal variation and catchment area during the wet season, or tidal variation and catchment area during the dry season. Salinity profiles were also correlated with the limiting estuarine ranges of two genera studied, *Sonneratia* L.f. and *Avicennia*. The upstream limit of *S. alba* was close to the 28ppt salinity position. The downstream limits of *S. lanceolata* and *A. integra*, were relatively close, just slightly upstream of 28ppt salinities. By contrast, the upstream limit of *A. integra* was much further upstream. These patterns reflect interspecific differences in physiological responses to seasonal fluctuations in salinity (cf. Ball, 1998).

Intertidal distributional gradients—zonation patterns

Mangroves are usually distributed across the intertidal profile from approximately mean sea level to the highest spring tides. There are some deviations from this pattern where mangroves occur well above the intertidal range, but these occurrences are exceptional and rare (e.g. van Steenis, 1963; Beard, 1967; Woodroffe, 1988). The distribution of species along the intertidal profile often forms distinct zones which match topographic contours (e.g. Macnae, 1968; Lugo & Snedaker, 1974). This is possibly indicative of the importance of tidal inundation. Different species often occur along particular sections of the intertidal profile, and they may be classified according to their intertidal position as: low, mid, or high. These positions are a reduction of five intertidal inundation classes described by Watson (1928), where: 'low intertidal' represents areas inundated by medium high tides and flooded >forty-five times a month (Watson classes 1 & 2), 'mid intertidal' represents areas inundated by normal high tides and flooded from twenty to forty-five times a month (Watson class 3), and 'high intertidal' represents areas inundated <twenty times a month (Watson classes 4 & 5). A species might therefore be known as a low- or high-intertidal specialist. Mangrove species are listed

in Table 1 and classified according to their intertidal position.

Smith (1992) reviewed many studies from countries in both the AEP and IWP (although chiefly in the latter), identifying zonation bands as a common pattern in mangrove distributions world-wide. It could be inferred that these zonation patterns have common controlling factors, but as Smith pointed out, the situation is more complex. Intertidal distributional patterns are influenced by a range of physico-chemical and biotic variables, and the zonation patterns differ between downstream and upstream transects, depending largely on different complements of species.

In Fig. 5, we present examples of distributional gradients across intertidal profiles from Panama and Australia. These show the common importance of upstream position influencing intertidal distribution of mangrove species. Species composition and intertidal distributions differ considerably for the three estuarine positions observed in these freshwater-dominated systems. Notable also in these examples is the occurrence in both systems of different *Rhizophora* species at downstream and intermediate estuarine locations, and the common occurrence of genera in front of *Rhizophora*: namely, *Laguncularia* in Panama, and *Aegiceras*, *Avicennia* and *Sonneratia* in Australia.

The importance of physiological influences along tidal profiles

Salinity gradients across intertidal profiles are complicated by factors such as evaporation of inundating tidal waters, ground water seepage and runoff. Slope of the profiles and climate are also important factors. For example, in drier climates, salinity gradients are more extreme, especially along profiles of very small slope. In northern Australian arid zones, vegetation-free patches (saltpans) occur within the mangrove intertidal zone, and these are typically larger in drier areas than they are in wetter places (Fosberg, 1961). In fact, in wet tropical areas they are often absent. The presence and extent of these bare areas is directly attributable to increased salt concentrations in sediments. Mangrove vegetation bordering these bare areas can be subject to localised dieback as a result of subtle year-to-year differences in rainfall. These limitations, like the others described, are species-dependent, resulting in species being zoned by their proximity to bare areas, and presumably, by their tolerance to high salt concentrations and aridity. This adds another dimension to intertidal distributions

and further disrupts the appearance of ordered species gradients in intertidal distributions.

Physiological attributes of species may also contribute to interspecific differences in distribution along tidally maintained gradients in environmental factors such as salinity and waterlogging (Ball, 1996). In the case of salinity, most mangroves grow best in relatively low salinities, but they differ in the range of salinities in which their maximal growth rates are sustained. In general, the greater the salt tolerance of a species, the slower is its growth rate under optimal salinity conditions. This occurs primarily because the less salt tolerant, and more rapidly growing species allocate more carbon to leaves such that they tend to have a higher ratio of leaf area to plant mass than more slowly growing, and more salt tolerant, species. These differences in architecture apparently relate to differences in water use characteristics which tend to become more conservative with increasing salt tolerance. Thus it appears that increasing salt tolerance occurs at the expense of growth and competitive ability under the low salinity conditions in which most species grow best. While many processes affect species distributions (Smith, 1992), species could become distributed differentially along salinity gradients because of interspecific differences in salt tolerance and because of the way in which physiological attributes associated with differences in salt tolerance affect competition for resources. Such interspecific differences in responses to salinity could lead to competitive exclusion along a spatial gradient in salinity (Ball, 1996) and to co-existence with temporal variation in salinity (cf. Ball, 1998).

The importance of faunal associates along tidal profiles

The distribution of mangrove species across the intertidal profile is influenced by associated fauna. For example, burrowing crustaceans promote growth of established trees by improving soil aeration, which reduces levels of harmful sulphides (Smith *et al.*, 1991). Fauna may also indirectly assist in establishment of propagules. Studies in Panama, where a dense fibrous root mat appeared to inhibit normal propagule establishment, indicate that *Rhizophora mangle* propagules established in crab burrows of a slightly larger diameter than the hypocotyl (Duke, Pinzón & Prada, in press).

By contrast, sesarimid crabs and molluscs damage propagules of selected species, influencing the

composition of forest communities (Smith 1987, 1992). Smith (1992) showed that propagules of *Avicennia* were selectively removed, or damaged, implying that this mangrove genus would be excluded where such predatory fauna occurred. Propagule consumption by grapsid crabs appears least in low intertidal areas and increases to maximal amounts in high intertidal areas. It was proposed that the commonly observed bimodal intertidal distribution of *Avicennia marina* in Australia and elsewhere, may be due to the sesarmid crabs living in the centre of the intertidal range of this mangrove species (Smith, 1987). The influence of these fauna is based on their presence, and their preference for propagules of particular mangrove species. This creates a situation where crabs which depend on mangroves bring about change to the composition and character of the forest stand.

Insects also attack and kill a substantial number of seeds and propagules of several mangroves, notably those with hard seed capsules, *Heritiera* and *Xylocarpus*, which are protected from certain crabs (Robertson, Giddins & Smith, 1990). Weevils burrowing into established *Rhizophora* propagules also have a similar effect on establishment and thus on the distribution of this genus. The full range of faunal influences remains to be identified and quantified, but these findings are instructive in demonstrating a higher level of complexity in the factors which influence species richness and distribution of mangroves.

The importance of dispersal ability and establishment along tidal profiles

Dispersal ability across the intertidal profile was suggested by Rabinowitz (1978) to be influenced by propagule size, however, there has been little or no support for this idea (Smith, 1992). It appears that a range of factors are important to dispersal on a local scale, possibly including propagule size, but also including: water quality; substrate condition; tidal position; the duration propagules can remain immersed before they sink; the time propagules take to germinate and produce roots; the resistance of propagules to, and tolerance of, damage caused by predators; and the general viability of propagules.

The importance of establishment, competition and light effects along tidal profiles

Establishment success for many mangroves appears to be aided by food reserves in their propagules, notably

of larger ones. There have been few assessments of the importance of propagule food reserves in establishment, and none on their influence on plant success in reaching maturity.

Light tolerance of seedlings differs for each species (Hutchings & Saenger, 1987). The importance of light depends on the amount available, where this is affected by cloud cover and seasons. There are at least four means by which a seedling of a shade intolerant species might become established: (1) by rooting in areas away from, or marginal to, existing stands; (2) by rooting under trees of species which have seasonal, low canopy density (includes deciduous trees, but not exclusively), and for the seedling to grow rapidly during these times (this might include partially shade tolerant undercanopy species; Ball, 1998); (3) by rooting in light gaps within existing stands (Smith, 1992); and (4) by possessing, as seedlings, greater tolerance of low light and thus growing within existing stands. In the latter case, plants need to acclimate to increased light as they reach the upper canopy.

In north-eastern Australia, Osborne & Smith (1990) found that some mangroves may derive unexpected benefits from light gaps. They observed that the amount of predation on *Avicennia marina* propagules in light gaps was a function of gap size, and predation decreased from 100% in small gaps (<100 m²) to less than 50% in larger gaps (>300 m²). This implied that *A. marina* might rely on regular, rapid establishment and growth, in an environment where other species (less favoured by predatory crabs) might become established under closed canopies and be well-advanced before gaps form. However, there is a problem here, since *A. marina* is incapable of growth in understorey shade (Ball & Critchley, 1982). This suggests a further interplay of influencing factors, involving light gaps as well as crabs, which together influence the distribution of *A. marina*.

The importance of stand support structure along tidal profiles

The root structure of mangroves in the low intertidal range is affected by their greater exposure to water movement and wind. Some species change their growth form in response to such conditions. For example, the genus which invariably dominates the low intertidal zone is *Rhizophora*. Trees of this genus are characterized by an above-ground, tangled network of sturdy prop roots. Furthermore, the trees can produce aerial anchor roots from their upper limbs, presumably when extra support is required. Such changes would take time, but

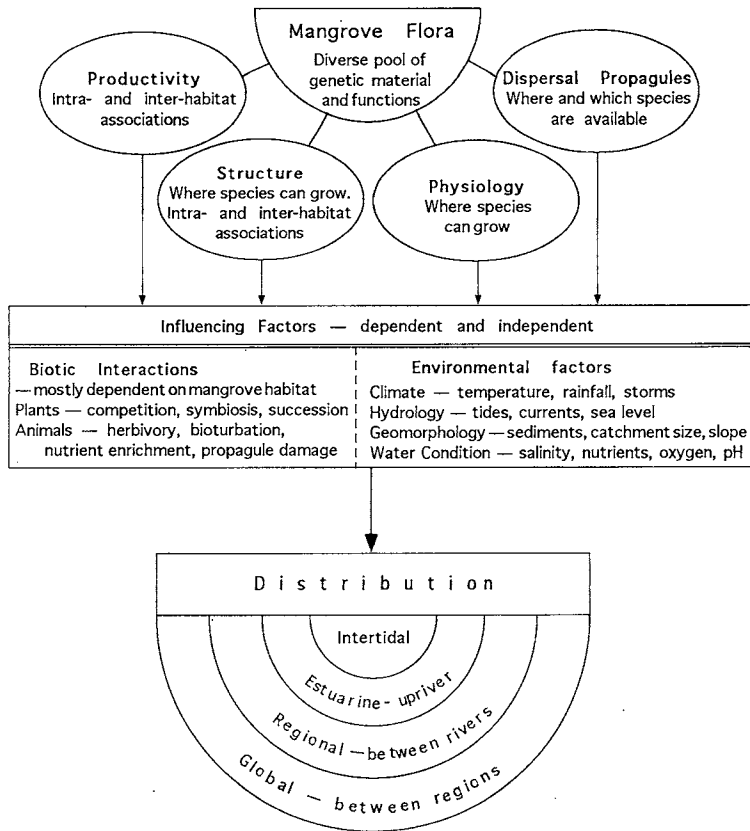


Fig. 6. Relationships between mangrove floristic, structural and functional diversity, and the range of factors chiefly influencing distribution, as discussed in this review.

where trees have grown up along exposed margins they develop more prostrate, sprawling statures, well-suited to resisting the effects of wind and waves and reducing water flow (Furukawa & Wolanski, 1996). By contrast, trees of the same species in inner parts of the stand often develop more erect stature of greater height and fewer support structures. The greater dominance of *Rhizophora* species in tropical mangroves, especially along low intertidal and in downstream estuarine positions, is apparently also highly influenced by this adaptability in developing support structures. By comparison, other species have only limited potential support structure development, and thus few species are able to grow in front of *Rhizophora*, except on stable or accreting edges and banks. It seems that shoreline stability is increased by the presence of *Rhizophora* (also see Wolanski *et al.*, 1990; Wolanski,

Mazda & Ridd, 1992) and that their stability promotes the establishment of other species both within, behind, and fronting them. This ability to sustain stands in fluctuating hydrological and depositional conditions largely explains the dominance of *Rhizophora* species at low intertidal locations and their influence on the presence and distribution of other species.

CONCLUSIONS

The distributions of mangroves are constrained by various physical, environmental and climatic factors (Fig. 6; Chapman, 1976; Hutchings & Saenger, 1987; Duke, 1992; Ball & Pidsley, 1995). If a species is present, then the environment must be suitable for it, but the opposite does not apply. Therefore, the presence of

particular species depends first on the proximity of source populations. Where a species exists in isolation of its conspecifics, this might be the result of past changes in climate, tectonic events, or both. This would apply particularly to populations distributed along continuous coastlines and through island archipelagos, or those which may have come together during periods of lower sea level. In such instances, tectonic changes may have a smaller influence, but in each case, environmental factors significantly influence distributions of mangrove plants.

This review of factors influencing distribution and species richness demonstrates that it would be unrealistic to expect simple assessments of one or two factors to have much general explanatory power. In an attempt to simplify this assessment, distributions and species richness were assessed at four geographic scales. But, while factors might be attributed to particular scales, there are many overlaps in both factors and effects. For example, effects of temperature are important in limiting global distributions by defining the effectiveness of major dispersal barriers toward the poles, while at a regional scale temperature serves to explain latitudinal gradients and species limits along north-south coastlines. Similarly, propagule dispersal is probably influential at all scales. Additional factors, include: availability of suitable habitats for establishment; establishment ability of each species; their physiological tolerance limits and growth responses; and their competitive abilities with respect to other species.

Essentially, all factors must act upon each plant in some way, and at some, or all, of the various stages of its life, from propagule development to dispersal, to establishment, to seedling growth, to reproductive years and maturation, to advanced age and death. As the factors act on the individual, they also act on each stand, and so the scale increases to include all influences considered in this review. Since mangrove plants are a pool of individual genetic entities related overall only by their ability to grow in the intertidal zone, they have understandably developed different attributes and strategies to live in this environment (Fig. 6), including: physical form and structure; physiological capabilities; productive capacity and growth; and reproductive development with dispersal of propagules. Each attribute is then influenced by a range of biotic and environmental factors which combine to determine the distributional patterns of each species in combination with others at global, regional, estuarine and intertidal scales.

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